Vol. 4 Issue- 1, September 2023 (e-ISSN: 2582-8223)

JUST AGRICULTURE
multidisciplinary e-Newsletter

ARTICLE ID: 79

Sex Reversal in Papaya (*Carica papaya*)

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Introduction

Papaya is one of the most nutritious and widely acceptable tropical fruit crop whose sex can be easily identified by the appearance of its flowers. Male papaya plant has elongated inflorescence having more number of flowers and female plant has few flowers with enlarged ovary. When farmers spot male plants in their orchard, there is no option other than removing them from field.

However, there are scientific reports pointing towards the influence of few environmental, genetical and chemical manipulation of flowering in Papaya. By exogenously applying a few growth regulators during the seedling/sapling stage, Ghosh and Sen (1975) and Jindal and Singh (1976) discovered a higher percentage of female plants in the population.Papaya farmers prefer growing hermaphrodite varieties so that they yield uniform fruits as a result of self-pollination. Due to global warming there will be unprecedented changes noticed in the temperature of earth. Effects of climate change can be very well observed in the crop papaya. For example, sudden heat prevailing in a region can induce sex-reversal leading the production of more male flowers on hermaphrodite trees. Drought, imbalance in the soil moisture conditions, nutrient status of the soil produces more masculine characters in papaya flowers thereby affecting the yield. Therefore, the future line of research regarding this undesirable character should be the identification of candidate gene correlating with sex reversal.

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Transitional forms of male &hermaphroditic papaya flowers

The hermaphroditic tree types, along with a race of fruitful male trees, generate a continuous range of flower types that are primarily bisexual but differ in the number of carpels, stamens, stigmatic rays, and other morphological characteristics. As a result, much study on sex reversal has been conducted on the hermaphroditic race of papaya which is profoundly influenced by differences in temperature and soil moisture conditions.According to Storey (1976), hermaphrodite plants may be "ambivalent," experiencing seasonal sex reversals. Even on the same plant, there might be variations in the number and type of blooms produced (Villegas, 1997). One of the most important plant sex classification was given by Storey in the year 1958. He classified papaya sex forms in to i) staminate, ii) teratological stamen, iii) reduced elongata, iv) elongata, v) carpelloid elongata, vi) pentandria, vii) carpelloid pentandria, viii) pistillata.

Staminate flowers are produced by true male plants whereas teratological stamens are produced by sex reversing male plants. Reduced elongate, elongata, carpelloid elongate, pentandria and carpelloid pentandria are normally produced by hermaphrodite plants. The most stable sex form is produced by female plants. Environmental conditions helps in the sex reversal phenomenon of male and hermaphrodite plants and these plants produces eight and six types of flowers during an year. The sex reversing male plants produces all 8 types of flowers and hermaphrodite plants produces 6 types of flowers except staminate and teratologicalstaminate flowers.

Genetics of sex reversal

According to Hofmeyer, 1938 & Storey, 1941, sex expression in papaya is controlled by a single gene with three alleles showing pleiotropic effect. M_1m, M_2m, mm represent androecious, hermaphrodite and female plants. Later, Storey (1953) reported that a single gene isn't responsible for sex determination in papaya but a complex of genes closely lying to the differential segments on the identical region of sex chromosomes. He also reported about two independent set of factors which could modify sex expression in papaya under some positive circumstances.According to Ram *et al.*, 1985, the existence of multiple allelism at the sex-determining locus in papaya has been discovered by genetic research using sex-reversing male and pure male and when sex reversing males were selfed, the ratio of sex reversing to pure male kinds was 3 to 1. On the other hand, the segregation ratio of 1:1 was seen when they were mixed with pure males. It is suggested that the genetic symbols for sex-reversing males be M_1^{RR} m or M_1^{Rr} m and for pure males be M_1^{rr} m.

Chromosomal influence of sex expression in papaya

Sex in papaya is regulated by X chromosome and two slightly different Y chromosomes. Female, male and hermaphrodite papaya has XX, XY and XY^h chromosomes respectively. Sequencing of entire male-specific region of Y (MSY) and hermaphrodite-specific region of Y^h chromosome (HSY) has been done by scientists. Studies of Liu *et al*. (2004) and Wang *et al*. (2012) concluded thatHSY and MSY are approximately 8.1 Mb that is 15 % of chromosome 1, which is the largest chromosome of the papaya and combination with X is suppressed giving male and hermaphrodite specific regions. Furthermore, YY and $YY^h$and Y^hY^h chromosomal combinations are non-viable. The Y and Y^h chromosomes share 99.6% of their similarities in the male-specific region of the Y chromosome (MSY), which was also sequenced and annotated. When papaya was domesticated by humans just 4000 years ago, the carpel suppressing gene on the Y chromosome underwent reverse mutation, leading to the development of Y^h (Van Buren *et al*., 2015).

Environmental influence of sex expression in papaya

Papaya is trioecious in nature expressing three sex forms such as male, female and hermaphrodite. Besides these predominant sex forms there are some intermediate sex forms which shows variation from the existing bisexual one. Storey (1941) classified papaya flowers in to five basic types (Type I, II, III, 1V, 1V+, V). Type I flowers are pistillate or female flowers which lacks stamen and have an ovoid ovary ending in a five lobed stigma, Type II flowers are hermaphrodite (pentandria) which have five functional stamen and a 5 ridged round ovary, Type III flowers are hermaphrodite (carpelloid) flower having six to 9 functional stamens and irregularly ridged ovary, Type 1V flowers are hermaphrodite (elongata) flower have ten functional stamens and elongated smooth ovary, Type IV+ flowers are hermaphrodite (barren) flower having 10 functional stamens but the abortion of pistil

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happens, becomes vestigial and lacks a stigma and Type V flowers are staminate and found as bunched inflorescence which have 10 functional functional stamens and are devoid of ovary. Apart from these five listed floral types some male and hermaphrodite trees undergoes a reversion of sex with respective morphologicalchanges and it varies with climatic and environmental changes. Cool temperature in spring time produces more female like, carpelloid (cat shaped fruits) in the flowers of hermaphrodite trees and high temperatures in summer can produce sterility with abortive pistils in papaya (Storey, 1958; Lange, 1961). Deformed fruits as a result of carpelloidy occur because of aggregation of stamens with the carpels of the flower and it has no particular commercial significance. MSXJ, a hybrid papaya has been found out to be free from this undesirable trait and it is a native of South-eastern Mexico (Mirafuentes *et al*., 2014). On male trees, the staminate flower clusters sometimes generate fertile, elongate-type hermaphrodite blooms in the terminal throughout winter (Iorns, 1908).

Epigenetic regulation systems influencing sex reversal related to low temperature

The interplay between the operation of sex determination pathways and epigenetic modifying mechanisms, including histone modification, DNA methylation, and microRNA, is likely what defines phenotypic sex expression. Finding the genes responsible for sex determination and differentiation can benefit from research on the epigenetic regulation of sexual reversals.According to Lin *et al*. 2016, at least two different epigenetic mechanisms such as histone modification and small RNAs are responsible for papaya sex differentiation. They found that 57 differentially expressed genes (DEGs) were upregulated in teratological staminate flowers (TSF) of papaya and were involved in the methylation of Histone H3 lysine 9 (H3-K9), which is a critical epigenetic marker for the establishment of heterochromatin formation and transcriptional silencing. Ovule identity gene (cpSTK) was expressed at higher concentrations on male-hermaphrodite sex reversal flowers, pointing towards the hypothesis of disappearance of gynoecium suppression function (GSF) from the sex determination pathway which is influenced mostly by the occurrence of low temperature. Up regulation of AUXIN RESPONSE FACTOR 5 in male-hermaphrodite sex reversal flowers also gave the conclusion of loss of female suppressing function on sex determination pathway. As a result major auxin efflux carriers regulate auxin distribution to the gynoecium.

Sex reversal with the help of gene silencing

The presence of a non-functional primitive pistil in the typical male papaya flower suggests that gynoecial organ development begins in the male flower and is suppressed later. Anatomical findings that suggested the primitive component was an extension of the receptacle from which carpels no longer differentiated supported this concept (Storey, 1967).Papaya has yet to yield a convincing sex determination gene, however it was suggested that the non-recombining area had at least two sex loci, a gynoecium suppression function (GSF) and a stamen promotion function (SPF) (Westergaard, 1958).Therefore, by inhibiting the gynoecium suppression function, it is possible to change a genetically male papaya flower into a phenotypical hermaphrodite.

Classical papaya sex evolutionary theory

According to the traditional hypothesis of plant sex evolution, dioecious and polygamous angiosperm with unisexual flowers evolved from perfect flowers directly through phylogenetic loss of one sex's organs' functions or organ loss itself (Yampolsky, 1925).The species with sex chromosomes that is most closely related to Arabidopsis is papaya and about 72 million years ago (MYA), papaya and Arabidopsis split from one another (Wikström *et al*., 2001). The family Caricaceae include 6 genera and 35 species, out of the 35 species, *Vasconella monoica* is monoecious, *Carica papaya* and *Vasconella cundinamarsensis* are trioecious and all the other 32 species are dioecious. Carica and Vasconcellea diverged about 27.5 MYA, according to molecular clock-based divergence estimates (Carvalho *et al*., 2012).An ZW chromosomal system may be present in *V. horovitziana*, according to research on the genome sizes of members of the Caricaceae family apart from XY chromosomal system. Therefore, papaya serves as an excellent model to study the evolutionary theory.

References

Carvalho, F. A. and Renner, S. S. (2012). Molecular Phylogenetics and Evolution- A dated phylogeny of the papaya family (Caricaceae) reveals the crop's closest relatives and the family's biogeographic history. *Molecular Phylogenetics and Evolution*, 65, 46-53.

Ghosh, S. P. and Sen, S. P. (1975). The modification of sex expression in papaya (*Carica papaya* L.). *Journal of Horticultural Science*, 50(2), 91-96.

Hofmeyer, J. D. J. (1938). Genetic studies of *Carica papaya* L. So. Africa Dept. Agr. For. Sci. Bui. 187.

Hofmeyr, J. D. J. (1939). Sex reversal in carica Papaya L. *South African Journal of Science*, 36(12), 286-287.

Iorns, M. J. (1908). Observations on change of sex in Carica papaya. *Science*, 28(708), 125-126.

Jindal, K. K. and Singh, R. N. (1976). Modification of flowering pattern and sex expression in *Carica papaya* bymorphactin, ethephon and TIBA; *Z. Pflanzenphysiol,* 78: 403-410.

Lange, A. H. (1961). The effect of temperature and photoperiod on the growth of *Carica papaya*. *Ecology*, 42(3), 481-486.

Lin, H., Liao, Z., Zhang, L. and Yu, Q. (2016). Transcriptome analysis of the male-to-hermaphrodite sex reversal induced by low temperature in papaya. *Tree genetics & genomes*, 12, 1-14.

Liu, Z., Moore, P.H. and Ma, H. (2004). A primitive Y chromosome in papaya marks incipient sex chromosome evolution. *Nature*, 427:348–352.

Mirafuentes Hernández, F. and Santamaría Basulto, F. (2014). MSXJ, híbrido de papaya sin carpeloidía para el sureste de México. *Revistamexicana de cienciasagrícolas*, 5(SPE7), 1297-1301.

Ram, M., Majumder, P. K. and Singh, B. N. (1985). Genetics of sex reversing male in papaya. *Indian Journal of Horticulture,* 42(1and2), 63-65.

Storey, W. B. (1938). The primary flower types of papaya and the fruit types that develop from them. *Proc. Amer. Soc. Hort. Sci*., 35:80-82.

Storey, W. B. (1941). The botany and sex relations of the papaya. Hawaii Agr. Exp. Sta. Bul, 87:5-22.

Storey, W. B. (1953). Genetics of papaya. *J. Hered.*, 44:70-78.

Storey, W. B. (1958). Modification of sex expression in papaya. *Hort. Adv.*, 2:49-60.

Storey, W. B. (1967). Theory of the derivations of the unisexual flowers of caricaceae. *Agron Trop.*, 17:273–321.

Storey, W. B. (1976). Papaya. In: Simmonds NW (Ed) Evolution of crop plants. Longman, London, pp 21–24.

Van Buren, R., Zeng, F., Chen, C., Zhang, J., Wai, C. M., Han, J. and Ming, R. (2015). Origin and domestication of papaya Y^h chromosome. *Genome research*, *25*(4), 524-533.

Villegas, V.N. (1997). *Carica papaya* L. In: EWM Verheij, RE Coronel, editors. Plant Resources of South- East Asia 2: Edible Fruits and Nuts. PROSEA Foundation, Bogor, Indonesia.